The Epivillafranchian carnivore *Pannonictis* (Mammalia, Mustelidae) from Sima del Elefante (Sierra de Atapuerca, Spain) and a revision of the Eurasian occurrences from a taxonomic perspective

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Abstract

Since the Early Villafranchian, the genus *Pannonictis* has been distributed in Eurasia from eastern China to the Iberian Peninsula. However, most of the finds of this large-sized mustelid are scant and fragmentary, resulting in a proliferation of names and unclear taxonomic history. *Pannonictis pliocaenica* and "*Pannonictis pilgrimi*" from Villány-Kalkberg are here considered as the same species, the latter being a synonym. The Asian representatives are among the most robust and present some anatomical differences. The recovery of new specimens from sites with well-known chronology and accurate stratigraphy is essential to clarify the taxonomic relationships among the several Plio-Pleistocene *Pannonictis* species described. The Sima del Elefante (Atapuerca, Spain) finds play a relevant role. *Pannonictis nestii* is a likely candidate as a last survivor of the genus, extending to the Late-Early Pleistocene. A review of the Eurasian occurrences of *Pannonictis* is presented, together with an attempt to establish a geographic and chronological picture of this genus that undoubtedly survived up to the Latest-Early Pleistocene. The Sardinian skull attributed to *Enhydrictis* "*galictoides*", is here placed as the only representative of this genus, and was likely confined to the Middle-Late Pleistocene in the Tusco-Sardinian paleobioprovince.

1. Introduction and historical framework

The Sierra de Atapuerca is a complex of Pleistocene cave deposits in Cretaceous limestones, which is geographically situated nearby the town of Burgos, northern Spain. Many of these fissures and caves were filled with sediments during the Quaternary, providing knowledge of ecosystems. The Sierra de Atapuerca represents one of the most complete Eurasian archaeo- and palaeontological sites, with an extraordinary richness of human fossils. All these recoveries are helping to understand the evolutionary processes during a period of around 1 million years (Arsuaga et al., 1993, 1997, 1999a, b; Carbonell et al., 1995, 1999, 2001; Parés and Pérez-González, 1995, 1999; Pérez-González et al., 1995, 2001; Bischoff et al., 1997, 2006; Cuenca-Bescós et al., 1997, 1999, 2001; García et al., 1997; García and Arsuaga, 1998, 1999, 2001; Falguères et al., 1999, 2001; van der Made, 1999a, b, 2001; Laplana and Cuenca-Bescós, 2000; Rosas et al., 2001, 2004; Cuenca-Bescós and Rofes, 2004; Huguet, 2007). Among the several Sierra de Atapuerca deposits, Sima del Elefante (also named Trinchera Elefante), in Trinchera del Ferrocarril, only a few metres away from Gran Dolina, has been excavated from 1996, continuing today. This site is a rich archaeological and palaeontological locality of Early and Middle Pleistocene layers, with evidence of human presence and abundant faunal remains. The section (Fig. 1) shows two main clayish infillings of sediments; one includes the

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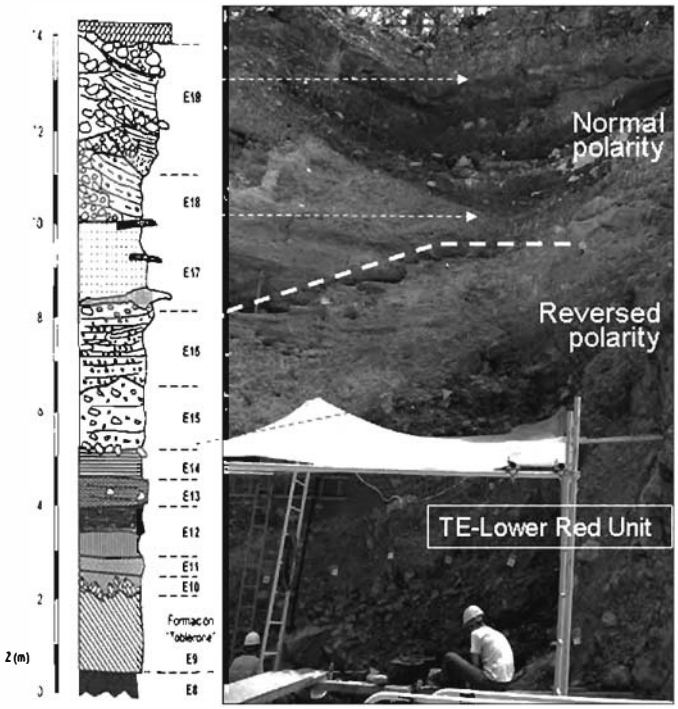

Fig. 1. Sima del Elefante (or Trinchera Elefante) section in Trinchera del Ferrocarril (Sierra de Atapuerca, Burgos). The Lower Red Unit (TE-LRU) includes the lowermost levels (8–14) where the *Pannonictis nestii* remains were recovered.

uppermost layers 18 and 19, and the other the lowermost ones (8 14), named the Lower Red Unit. Paleomagnetic analyses within the section revealed reversed polarity in level 16 and all layers below, and normal polarity in levels 17 19 (Parés et al., 2006). These results support the assignment of the Lower Red Unit layers to the Matuyama Magnetochron which is consistent with the Early Pleistocene age (Waalian) proposed by Cuenca-Bescós and Rofes (2004), based on the insectivore association. The rodent association is similar to that recorded in other South-European localities of Latest Villafranchian or Epivillafranchian age. Trinchera Elefante-Lower Red Unit (TE-LRU) is thus older than the deepest exposed levels of Trinchera Dolina (TD-3 to TD-6, ca. 0.78 0.9 ka), and thus older than 1 million years (Cuenca-Bescós and García, 2007). The TE-LRU represents some of the earliest evidence of human activity in Europe, shown by the presence of Mode 1 stone tools (Rosas et al., 2001, 2004). The study of the palaeontological context implies a deeper knowledge on the paleoecology of the early human settlement in Eurasia. However, more knowledge about the stratigraphic range of *Pannoncitis*, which survived up to the Latest-Early Pleistocene, is needed.

Kormos (1931) described the genus *Pannonictis* as one species, *Pannonictis pliocaenicus*, from a number of Hungarian localities (Villány, Beremend, Csarnóta, and Püspökfürdö), all of which date to the Late Pliocene. In a later publication, Kormos (1933) referred part of the material to a second, smaller species, which he named *Pannonictis pilgrimi*. Since then, some authors (Viret, 1954; Willemsen, 1988) have considered the small form as a synonym of another described mustelid (*Enhydrictis*), while others (Ficcarelli and Torre, 1967) kept them as separate taxa. Furthermore, there is disagreement on the biochronological range of this genus as well as its paleoecological implications. The controversy and proliferation of names for this mustelid will continue increasing unless a thorough analysis of the group is undertaken. Here a preliminary approach is proposed to address the most important questions raised by *Pannonictis*, including most of the Eurasian occurrences.

2. Materials and methods

This study is based on comparative morphological and metrical analyses of the recently discovered remains from the Early Pleistocene deposits at Sima del Elefante (level 9 TE9 of TE-LRU) in the Sierra de Atapuerca and the extensive *Pannonictis* collection (*P. pliocaenica* and *P. pilgrimi*) stored at the Hungarian Geological Institute at Budapest ($n > 90$) (Figs. 2 and 3). These two species described by Kormos (1931, 1933), were recovered from the Villány-Kalkberg (including the *P. pilgrimi* type-species Ob 3618), Beremend (*P. pilgrimi* UP606) and from Csarnóta 1 (*P. pilgrimi* Ob 3969, first assigned to a new genus *Xenictis*). Only a minimal part of this material has ever been published, and no further studies or revision of this material was undertaken. The TE-LRU remains constitute an important contribution to the knowledge of this taxa for several reasons: (a) the very precise information about its age, placed between 1.3 and 1.0 Ma (Rosas et al., 2004; Parés et al., 2006; Cuenca-Bescós and García, 2007); (b) paleoecological conditions can be inferred from the analysed insectivore fauna (Cuenca-Bescós and Rofes, 2004); and (c) the two skulls show considerable size differences (likely attributable to sexual dimorphism), which can be applied to better understand the variability of the group. Moreover, additional published material from related Eurasian sites was included in this comparison. Table 1 and Fig. 4 show the known sites where any specimens were assigned to genus *Pannonictis* or *Enhdryctis* by different authors. The localities are divided in the text (and in Table 1) into several Eurasian geographic regions as follows: (1) East and Central Asian; (2) Black Sea and Transcaucasian; (3) South-East European; (4) North and Central European; and (5) Mediterranean.

3. *Pannonictis* morphology: remarks on taxonomy

3.1. Sima del Elefante (LRU) remains

The cranial remains recovered from TE-LRU correspond to two individuals of different sizes. A more detailed analysis of the anatomical features is given in García and Howell (in press). Here, only a general description of the most distinctive traits is provided for comparative

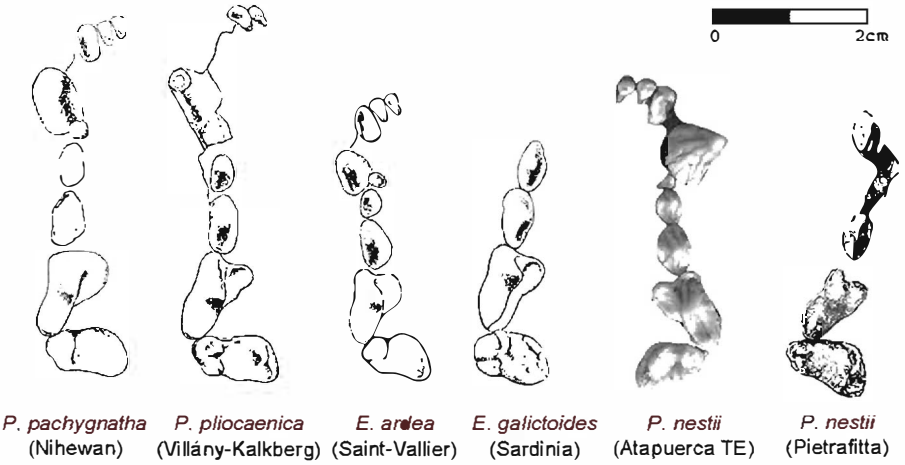

Fig. 2. *Pannonictis* cranial remains from Sima del Elefante (TE-LRU) (Sierra de Atapuerca) compared to other localities. *P. pachygnatha*, *P. pliocaenica*, *E. ardea* and *E. galictoides* are taken from Ficcarelli and Torre (1967); *P. nestii* from Pietrafitta from Rook (1995).

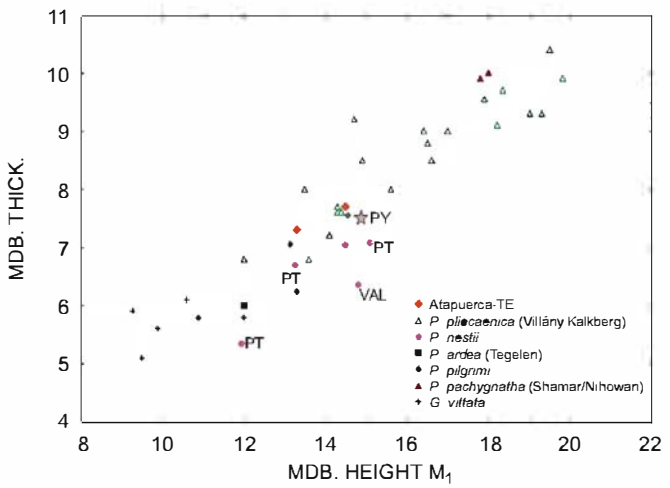

Fig. 3. Scatter diagram. Height of mandibular rami (on M_1) versus mandibular thickness (on M_1). *P. pachygnatha* are all among the more robust. The star symbol represents Palan-Tyukan, first published as *E. ardea* but that coincides well with the *P. nestii* values and the more slender *P. pliocaenica* ones. The Sima del Elefante (TE) specimens have intermediate robustness. PT: Pietrafitta, VAL: Valdarno. Variables in millimetres.

discussion: long occipital, short and stout muzzle (relative to the total skull length), expanded in the area of maxillary zigomatic process; post-orbital constriction (relatively) broad. I^3 separated from the canine by a tiny diastema. Canines are strongly and deeply wrinkled. P_1 present in the left side of the largest individual; unicusped P_2 and P_3, moderately robust, with a high and straight principal cusp, morphologically similar, P_3 being larger. In occlusal view, both show a rhomboid profile, as they are medially broader. P_4 presents a high and strong paracone. The protocone is a shallow basin, and extends up to approximately half the length of the tooth. Its lingual margin is curved and is surrounded by a slightly raised enamel ridge enclosing the shallow basin. In frontal view, a large infraorbital foramen is located above the anterior part of the P_4. The upper canines are straight, sharp and large (felid-like), strongly and deeply furrowed and wrinkled, with a characteristic anterolateral deep groove covering two-thirds of the crown.

The mandibles are low and massive. The ascending ramus, especially robust at the base, presents a deep masseteric fossa that extends anterior to the M_2 reaching the posterior edge of M_1. The mandibular condyle is located at the level of the teeth raw. The pterigoids insertions are well developed and the coronoid process is relatively small. The lower canines even more strongly and deeply wrinkled than the upper ones; they are curved sharply upward (hook-like) and show a well-raised collar-like cingulum, above the base of the crown. The lower carnassial presents a metaconid smaller than the other two cuspids of the trigonid but is stout and placed separately. The talonid is simple and flat (not narrower than the trigonid) with only one hypoconid in the buccal side, and neither entoconid nor hypoconulid remain. The talonid has a lingual rim (typical of representatives of genus *Pannonictis*). M_2 is small and nearly circular.

3.2. *Comparisons and discussion*

The presence of P_1 is variable within the Villany-Kalkberg collection: it is present in Pietrafitta and Saint Vallier, and absent in *Enhydrictis galictoides* from Sardinia. The extant representatives of the *Galictis* group, now living in Central and South America (*Galictis cuja* and *Galictis vittata*) always lack P_1. This could be interpreted as a tendency towards the loss of P_1 within the Grisoninae. The P_2 and P_3 studied from Villány-Kalkberg show a more elliptical outline than the TE specimens, and the principal cusp is placed slightly more anterior. The morphology and position of the principal cusp from the TE-LRU P_4 is also observed in the *Pannonictis pliocaenica* collection from Villány-Kalkberg, and Pietrafitta while *E. galictoides* from

Table 1
Eurasian localities with presence of *Pannonictis* or *Enhydritis* species (following each author's nomenclature)

Age range	Chronostratigraphic unit/ approximate age	Mediterranean area	West and Central Europe	South-East Europe	Black Sea and Transcaucasia	East Asia	Reference
Late Pleistocene		Monte Tuttavista IX (Sardinia, Italy)					Abbazzi et al. (2005)
		Monte San Giovanni (Sardinia, Italy)					Forsyth Major (1901)
		Oletta cave (Corsica, France)					Ferrandini and Salotti (1995)
		Grotta Dragonara (Sardinia, Italy)					Masseti (1995)
Epivillafranchian (1.3–0.9 Ma)	Late-Early Pleistocene	Huéscar 1 (Spain)					Alcalá and Morales (1989), Hernández Fernández et al. (2004)
	Late-Early Pleistocene			Betfia 5 (Romania)			Jánossy (1986)
	1.1–1.3 Ma	TE-LRU (Atapuerca, Spain)					Parés et al. (2006), García and Howell (in press)
	1.3 Ma			Betfia = Püspökfürdö (Betfia 2–4) (Romania)			Jánossy (1986), Terzea (1996)
Plio-Pleistocene	1.4 Ma	Pietrafitta (Italy)					Rook (1995), Ambrosetti et al. (1987)
	Early Pleistocene		Deutsch-Altenburg 2C1 (Austria)				Rabeder (1976)
	Late Villafranchian (Tasso/Farneta; 1.7–1.4 Ma)			Libakos (Greece)			Spassov (2000)
	Late Villafranchian (Tasso/Farneta; 1.7–1.4 Ma)	Mugello (Val di Sieve, Italy)					Abbazzi et al. (1995)
	1.8–1.5 Ma			Villány 5 (Hungary)			Kormos (1931), Jánossy (1986)
	1.7 Ma	Casa Frata (Italy)					
	MN 17 (1.8 Ma)		Tegelen (the Netherlands)				Steensma (1988)
	LateVillafranchian (1.8 Ma)				Palan-Tyukan (Azerbaidzhan)		Sotnikova and Sablin (1993), Vislobokova et al. (1993)
	MN 17 (1.8 Ma)						Abbazzi et al. (2005)

Table 1 (*continued*)

Age range	Chronostratigraphic unit/ approximate age	Mediterranean area	West and Central Europe	South-East Europe	Black Sea and Transcaucasia	East Asia	Reference
		Monte TuttavistaVII (Sardinia, Italy)					
	MN 18 Late Villafranchian (2.0–1.8 Ma)	Olivola (Val di Magra, Italy)					
	MN 17 (1.95 Ma)			Varshets (Bulgaria)			Spassov (1997, 2000, 2003)
	MN 17 (1.95 Ma)		Saint Vallier (France)				Viret (1954)
	MN 17–18 (2.0–1.5 Ma)			Csarnóta 1 (Hungary)			Kormos (1931), Jánossy (1986)
	MN 17–18 (2.0–1.5 Ma)			Beremend (Hungary)			Kormos (1931), Jánossy (1986)
	MN 17–18 (2.0–1.5 Ma)			Villány 3 (Villány-Kalk.-Nord, Hungary)			Kormos (1931), Jánossy (1986)
	Late-Middle–Early-Late Villafranchian (1.8–1.7 Ma)	Upper Valdarno (Italy)					Martelli (1906), Ficcarelli and Torre (1967)
	Late Pliocene (2.4 Ma)		East-Runton (Great Britain)				Newton (1890), Stuart (1982), Gibbard et al. (1991)
	MN 16b		Perrier-Étouaires (France)				Schaub (1949), Hemmer et al. (2004)
	Middle Villafranchian	Villaroya (Spain)					Villalta (1952)
	Khapry faunal unit (2.2–2.6 Ma)			Khapry (SE Russia)			Sotnikova et al. (2002)
	Early Villafranchian	Arondelli (Italy)					Berzi et al. (1970)
	Pliocene	Casa Sgherri (Lower Valdarno, Italy)					Marcolini et al. (2000)
	Villafranchian s.l.	Monte Pellegrino (Italy)					Kotsakis (1985)
	Villafranchian					Yushe (China)	Teilhard de Chardin and Leroy (1945)
Ruscinium	Villafranchian					Nihewan (China)	Teilhard de Chardin and Piveteau (1930)
	MN 16a (2.6 Ma)					Shamar (Mongolia)	Sotnikova (1980), Vislobokova et al. (1993)
	MN 15				Etulia (Moldova)		Sotnikova et al. (2002)
	MN 15		Wölfersheim (Germany)				Morlo and Kundrát (2001)

The occurrences are divided by geographic regions and by chronological periods. Sources on the taxonomic attribution and the chronology of the sites are also included.

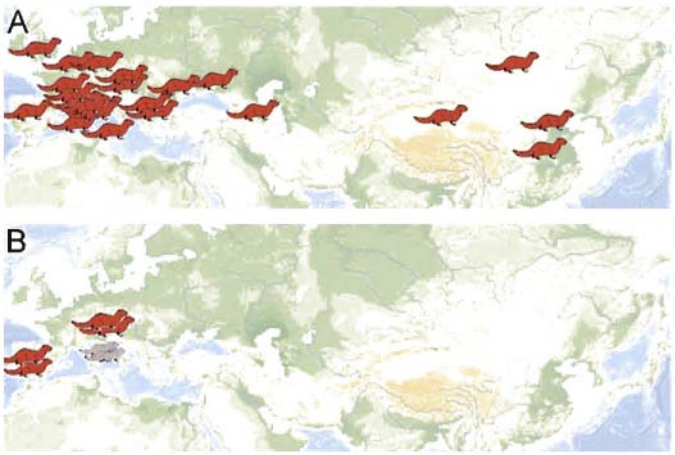

Fig. 4. (A) *Pannonictis/Enhydrictis* Villafranchian Eurasian sites (from 2.6 to 1.4 Ma). Asian occurrences: Shamar (Mongolia), Nihowan and Yushe (China); Black Sea and Transcaucasian occurrences: Palan-Tyukan (Azerbaidzhan), Khapry (Russia); Etulia (Moldova); European occurrences: Varshets (Bulgaria); Libakos (Greece); Villány-Kalkberg, Csarnotá and Beremend (Hungary); Tegelen (the Netherlands); Red Crag (Great Britain); Saint Vallier and Étouaires (France); Valdarno, Monte Pellegrino, Monte Tuttavista VII, Pietrafitta, Mugello and Arondelli (Italy); Villarroya (Spain). Sources and chronology are shown in Table 1. (B) *Pannonictis/Enhydrictis*, (a) Epivillafranchian sites (from 1.3 to 0.9 Ma)—in grey: Betfia (Püspökfürdö = Betfia 2–4) and Villány 6 (Villány-Kalkberg)—both in Hungary; Huéscar 1 and Atapuerca TE-LRU (Spain); (b) Late Pleistocene sites (with *Enhydrictis*): Monte Tuttavista IX, San Giovanni (Capo Figari) (Italy), Grotta della Dragonara (Sardinia) and Oletta cave (Corsica, France). Sources and chronology are shown in Table 1.

Sardinia, shows a shorter protocone, which only extends up to approximately one third the length of the tooth. The M_1 of TE-LRU does not show a rectangular shape, as observed in *P. pliocaenica* and *Pannonictis pachygnatha*, but resembles the specimen from Pietrafitta, differing from the Sardinian *Enhydrictis*, which is expanded and rounded (Fig. 2). The M_1 presents an anterior border straight while the lingual edge is broader at the mid line of the tooth, which results slightly more expanded in the middle area.

The coronoid processes are smaller in the TE-LRU mandibles than the *P. pachygnatha* representatives, which are very robust. Kormos (1933) found that the M_1 of *Enhydrictis* and *Pannonictis* differed from the metaconid of *E. galictoides*, situated in line with the protoconid, whereas in *Pannonictis* it had a more posterior position.

After analysing the large collection of *Pannonictis* collection from Villány-Kalkberg, Csarnotá 1 and Beremend ($n > 80$ remains), attributed to *P. pliocaenica* and *P. pilgrimi*, no morphological differences between the fossils assigned to both species were detected (García and Howell, in press). For example, the lingual rim at M_1, lacking in the holotype of *P. pilgrimi*, as a diagnostic feature (Kormos, 1933), is clearly observed in a fresh specimen, as in all *P. pliocaenica*. Also, no major differences were found between P_2 and P_3 of *P. pilgrimi* and *P. pliocaenica*, in the dimensions or the position of the cusps.

Fig. 3 includes remains of other species of the genus as *Pannonictis nestii* and *P. pachygnatha*, as well as *E. galictoides*, the specimen from San Giovanni (Sardinia). Some of them have been ascribed to *Enhydrictis*, but all fall within the *P. nestii* group. Extant South America representatives of genus *Galictis* (*G. vittata* and *G. cuja*) are also included.

4. Distribution and chronology of *Pannonictis* and *Enhydrictis* in Eurasia

The Eurasian record of *Pannonictis* and *Enhydrictis* remains has been divided in five main regions, from eastern China to the Mediterranean margin, including a total of 36 localities (Fig. 4). These groups include all the sites mentioned in Table 1, which are here also assigned to different chronological periods. All species assigned to both genera are included in this selection. It is proposed that all the fossil remains from Early Pleistocene sites, even slightly earlier, up to around 2.6 Ma should be grouped in only one genus.

4.1. East and Central Asian record (China, Mongolia)

The fossil record from this area includes three sites, Nihewan (Teilhard de Chardin and Piveteau, 1930), Yushe (Teilhard de Chardin and Leroy, 1945) and Shamar (Sotnikova, 1980). The two sites from China are characterised by Villafranchian faunas. The Lower Villafranchian deposits of Shamar (northern Mongolia) have yielded remains originally described as *Mustela* (= *Pannonictis*) *pachygnatha* (PIN 3381-197) (Sotnikova, 1980). The fossil-bearing horizon at Shamar is directly above basalts dated to about 3.1 ± 0.2 Ma (Vislobokova et al., 1993; Hemmer et al., 2004), and the fauna is referred to zone MN 16a (Vislobokova et al., 2001). An age range between 3.1 and 2.6 Ma is considered for the Shamar faunal assemblage.

Recently, Qiu et al. (2004) have proposed a new genus name for the mustelids described by Teilhard de Chardin and Piveteau (1930) from Nihewan, based on some dental morphological differences with *Pannonictis* from the Hungarian deposits. Following this study, these remains would now be mentioned as *Erictis pachygnatha*. However, although the main diagnostic traits are found in M_1 and P_4 following Qiu et al. (2004), these are not detected in any of the specimens of the Villány-Kalkberg collection revised by one of the authors (N.G.).

4.2. Black Sea and Transcaucasian record (Moldova, SE Russia, Azerbaijan)

The first data attributed to *Pannonictis* from the European part of the former Soviet Union are placed at the MN 15, at Etulia (Moldova). Here a specimen (GIN 428-218) is assigned to *P. pliocaenica* by Sotnikova et al. (2002), occurring somewhat later (MN 16) in the Asian part and in Mongolia (Vislobokova et al., 2001). The Khapry sequence (Azov region, SE Russia) has yielded

remains of large mammals from four sites. A fragmentary anterior left part of a mustelid skull (RSU-1327) and a right ramus (RSU-98/2034) coming from the Liventsovka quarry, were assigned to *P. nestii* (Sotnikova et al., 2002). The Khapry sequence formed during a single sedimentary cycle and the fossils were defined by Gromov (1948) as the Khapry Faunal Unit of the Late Pliocene age (Middle Villafranchian West European fauna = Zone MN 17) (Sotnikova et al., 2002). Palan-Tyukan (Azerbaijan) yielded a mandible remain (no. 34173) originally assigned to *Enhydrictis ardea* by Sotnikova and Sablin (1993). However, the massive index (height mandible corpus below M_1/breadth mandible corpus at M_1) of the Palan-Tyukan specimen coincides well with others *P. nestii* representatives (Fig. 3), in contradiction to the resulting comparisons from the first study, which grouped Palan-Tyukan together with *E. ardea* from Tegelen and apart from *Pannonictis* from Etulia (Moldova). However, there is no evidence from the morphological description (Sotnikova and Sablin, 1993, p. 138) or robustness proportions for any argument to separate this specimen from *Pannonictis*. Etulia and Khapry are placed between 2.2 and 2.6 Ma (Sotnikova et al., 2002), somewhat older than the Palan-Tyukan of around 1.8 Ma (Vislobokova et al., 1993). The dimensions are intermediate between those two and the Tegelen specimen, which is the most slender.

4.3. South-East European record (Hungary, Romania, Greece, Bulgaria)

From the Hungaryian complex of cavities at Villány 3 (Villány-Kalkberg-Nord) comes the most complete collection of *P. pliocaenica* described by Kormos (1931). Some smaller remains were attributed to *P. pilgrimi* and a left mandible fragment (with P_4 M_1 M_2) stored at the Royal Hungarian Geological Survey was the holotype (Ob 3618) (Kormos, 1933). However, this different specific attribution is not accepted here. Csarnóta 1 and Beremend (both from Hungary) also yielded *Pannonictis* remains. The age of Villány 3 (the richest locality) probably ranges from 2.0 to 1.5 Ma (Jánossy, 1986) and probably the fossil-bearing strata correspond to a rather long period of time with more than one faunal association included there (Spassov, 2000). It is broadly accepted that its fauna belongs to the Saint Vallier Unit (MN 17 18). The Villány 5 assemblage is probably more modern, and some authors place it at around 1.8 Ma (Spassov, 2000). Betfia (Bihor, Romania) is a cave deposit from 1.81 to 0.78 Ma, where *P. pliocaenica* remains were recovered (Terzea, 1996). From Libakos (Northwest Greece) two canines were attributed to *E. ardea* by Steensma (1988) based on their smaller dimensions than the Villány ones and closer to Tegelen. However, the sample from Villány used by this author is taken from Kormos (1931) and is considerably smaller than the sample used here ($n = 32$) which shows a wider size range ($LC_i = 7.3$ 11.0; $WC_i = 5.1$ 8.3) within which the Libakos specimen would be included ($LC_i = 8.7$, 8.8; $WC_i = 5.5$, 5.6, Steensma, 1988). The site of Varshets (Northeast Bulgaria), is a cave deposit that has yielded abundant mammal megafauna typical of zone MN 17 and similar to La Puebla de Valverde, Saint Vallier or Chilhac. *Pannonictis ardea* is included among this rich association (Spassov, 1997, 2000).

4.4. North and Central European record

The type specimen of *P. ardea* originates from Côte d'Arde, in Perrier-Étouaires (Puy-de-Dôme, France) and consists on one left mandible with M_1. This was first described as *Mustela ardea* Bravard, until Schaub (1949) adopted the *Pannonictis* genus given the similarities with the *P. pilgrimi* fossils published by Kormos (1933). The fauna from Perrier-Étouaires is allocated to zone MN 16b, therefore corresponding biostratigraphically to the Italian Montopoli Faunal Unit (Gliozzi et al., 1997; Hemmer et al., 2004). From the Pliocene site of Saint Vallier (France), a skull and mandible (QSV-150) was attributed to *E. ardea* (Bravard) by Viret (1954). Schreuder (1935) published a lower canine from the Tegelen Clay (the Netherlands) and Willemsen (1988) a few more remains which he separated between *Enhydrictis* and *Pannonictis*, based on size criteria principally. There is also evidence of *P. pliocaenica* from Weybourn Crag Red Crag (Great Britain) (Stuart, 1982) which represents the northernmost occurrence of this taxon in Eurasia.

4.5. Mediterranean record

The richest area with *Pannonictis* remains is the Italian peninsula and in particular the "Tusco-Sardinian paleobioprovince" located on the peri-Tyrrhenian side of Italy. The holotype of the species *P. nestii*, first described by Martelli (1906), consists of a mandible (IGF 916) and originates from the Upper Valdarno (Tuscany) locality with a chronology of around 1.8 1.7 Ma. Furthermore, a number of Italian sites of Villafranchian age (Monte Pellegrino, Casa Sgherri in Lower Valdarno, Arondelli near by Villafranca d'Asti, Mugello in Val di Sieve, Olivola in Val di Magra and Casa Frata in Upper Valdarno, have yielded fossil remains of *Pannonictis* (Table 1). *Pannonictis* remains also were described from Monte Tuttavista VII-Mustelide (Sardinia) with an Early Pleistocene faunal assemblage (Abbazzi et al., 2005).

The site of Pietrafitta is located in Central Italy (Umbria). Here an incomplete and very fragmentary skull (1749) and one complete mandible (1750) among some isolated teeth were described as *P. nestii* (Rook, 1995). The age of this site is placed at the Late-Early Pleistocene, at around 1.4 Ma (Ambrosetti et al., 1987). Villalta (1952) assigned to *Lutra sinerizi* nova.sp a fragmentary mandible from the Villarroya (Spain) Villafranchian site, which Viret (1954) reassigned to *E. ardea*.

A skull was recovered from a fissure in Monte San Giovanni (Sardinia, Italy) and was first described by

Forsyth Major (1901) and named as *E. galictoides*. The age of this fossil is uncertain but was suggested to be more recent than the *Pannonictis* specimens found in mainland Europe. A number of similar fossils were recovered from nearby sites attributed to the Late Pleistocene, or in some cases to the Late-Middle Pleistocene. Some of these localities of Late Pleistocene age are: Monte Tuttavista IX, Grotta della Dragonara (Sardinia, Italy) and Oletta cave (Corsica, France) (Ferrandini and Salotti, 1995; Abbazzi et al., 2005).

The "Tusco-Sardinian paleobioprovince" (Tuscany and Sardinia) was connected in the Messinian but also during several periods of the Pleistocene when sea level drop and temporary emergence of marginal lands allowed different phases of faunas to pass from mainland Italy. The idea, previously proposed by other authors as Pilgrim (1932), that "*E. galictoides*" was derived from a primitive ancestor of the genus *Pannonictis* (i.e. *P. nestii*) which lived in Eurasia (including the Mediterranean region) is supported in this context of isolation.

5. Results and discussion

The finds from the Sierra de Atapuerca at TE-Lower Red Unit with an age ranging between 1 and 1.4 Ma are assigned to *P. nestii* (a male and a female individual). The occurrence of *Pannoncitis* in Trinchera-Elefante (LRU) provides knowledge about the Eurasian stratigraphic range of these taxa, which survived until the Epivillafranchian.

After morphological and metrical analysis, several conclusions about the different species were reached: *P. nestii* (= *Enhydrictis ardea*) is a smaller and more slender species of the *Pannonictis* genus. The Villány-Kalkberg large sample provides support for the hypothesis of sexual dimorphism instead of two separate species, representing the larger representatives of the sample (*P. pliocaenica*) males, and the smaller (*P. pilgrimi*), females. For the members of the genus *Pannonictis*, a high sexual dimorphism is proposed. All mustelids exhibit pronounced sexual size dimorphism (Moors, 1980) and even Dayan and Simberloff (1994) considered males and females (of same species) to be functionally distinct "morphospecies". Hence, the division could have been done in many other ways as well as into only two groups, a large and a smaller group representing sexually different individuals. This study suggests *Pannonictis* and *Enhydrictis* are separate genera, although closely related, the latter being represented only by the Sardinian specimen. *E.* "*galictoides*" from Sardinia could be a relict form of an old genus, confined to the Late Pleistocene in the Tusco-Sardinian paleobioprovince. *Pannonictis* (= *Eirictis*) *pachygnatha* is a more robust species, with specific dental and mandible differences.

Pannonictis remains have been recovered from 36 Eurasian sites from eastern China to the Mediterranean margin and the Iberian Peninsula. The localities are divided in five main regions, which show this group was widespread during the Plio-Pleistocene in Eurasia. The division also shows a gap of fossil sites in western Asia. In some cases the absence of this mustelid in the faunal associations is attributed to ecological reasons, but some more likely reasons are taphonomic bias or a lack of deeper knowledge, particularly with material assigned to Mustelidae indet.

A strict aquatic life of *Pannonictis*, comparable to the style of otters, is not likely, but habitats close to river courses are suggested, similar to those of their phylogenetic descendant, the American *Galictis* species. The occurrence of *Pannonictis* ranges from slightly before 2.6 Ma until the Epivillafranchian (between 1. 3 and 0.9 Ma), but is more commonly recorded between 2.6 and 1.4 Ma (with 25 localities). Analyses of rich deposits (especially Asian) included in this time-span and with a fluvial context (such as Dmanisi, Kotsakhuri, Kopaly and others of the time-span around 1.8 Ma; see Kahlke, 2006), should be undertaken to fill this gap. The Epivillafranchian period (for detailed information, see Kahlke, 2004, 2006) represents the latest occurrence of this group, with five localities yielding *Pannonictis* remains, but it is recorded only in the South-East European and the Mediterranean regions. Finally, only the Mediterranean region includes presence of the Late Pleistocene descendent, *E.* "*galictoides*", probably as a relict form descendent of a mainland *Pannonictis* ancestor.

Acknowledgements

We thank L. Kordos for allowing access to the Villany-Kalkberg collections of *Pannonictis* stored at the Geological Institute of Hungary, and under his care. He also provided generous assistance during visit to Budapest. We are also grateful to the Sima del Elefante excavation team. Special thanks to R.-D. Kahlke for providing important references and comments on the biochronology of the sites involved in the study and on the Epivillafranchian topic. We are also indebted to Marina V. Sotnikova who provided enriching recommendations and comments. This study was supported by the Ministerio de Ciencia y Tecnología (BOS-2003-08938-C03-01) and Fundación Atapuerca granted to R. Huget.

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